

Distributed and Overlapping Cerebral Representations of Number, Size, and Luminance during Comparative Judgments

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Summary

How are comparative judgments performed in the human brain? We scanned subjects with fMRI while they compared stimuli for size, luminance, or number. Regions involved in comparative judgments were identified using three criteria: task-related activation, presence of a distance effect, and interference of one dimension onto the other. We observed considerable overlap in the neural substrates of the three comparison tasks. Interestingly, the amount of overlap predicted the amount of cross-dimensional interference: in both behavior and fMRI, number interfered with size, and size with luminance, but number did not interfere with luminance. The results suggest that during comparative judgments, the relevant continuous quantities are represented in distributed and overlapping neural populations, with number and size engaging a common parietal spatial code, while size and luminance engage shared occipito-temporal perceptual representations.

Introduction

How are continuous quantities such as size, weight, luminance, or number represented in the human brain? What processing stages lead from a sensory representation to an explicit internal continuum that supports comparative judgments (e.g., longer than a pen) and numerical measurements (e.g., about 25 cm long)? The neural bases of comparative judgments have been extensively studied in the numerical domain. When comparing two numbers, performance is slower and less accurate when the numbers are close (e.g., 59 and 61) than when they are further apart (e.g., 39 and 81) (Moyer and Landauer, 1967). Several brain-imaging studies have used this numerical distance effect to individuate the cerebral bases of the internal representation of numerical quantities (Dehaene, 1996; Pinel et al., 1999, 2001). Because this effect is additive with respect to notation (Arabic or number names) and response preparation factors, a serial stages model of the comparison task has been previously proposed (Dehaene, 1996), where the central stage is the comparison operation performed on an abstract representation of number magnitude. Extension of the additive-factors method to an fMRI design isolated the correlates of this notation-independent com-

parison stage in the parietal cortex, more specifically in the intraparietal sulcus and precuneus (Pinel et al., 2001).

In the present paper, we examine to what extent those results, which were obtained with symbolic Arabic numerals, can be extended to other nonsymbolic continua such as size and luminance. One possibility is that comparative judgment on each continuum requires access to a dedicated subregion of the intraparietal cortex. Indeed, the hypothesis that a subregion of intraparietal cortex holds a category-specific representation of number is coherent with many other imaging studies of number processing (Stanescu-Cosson et al., 2000; Burbaud et al., 1999; Pesenti et al., 2000; Naccache and Dehaene, 2001; Menon et al., 2000; Eger et al., 2003; Fias et al., 2003). A recent meta-analysis of eight fMRI studies using various tasks (number comparison, subtraction, approximation, or estimation) and methods (subtraction, priming, correlation) points to the horizontal segment of the bilateral intraparietal sulci (IPS) as playing a special role in the internal representation of numerical quantities (Dehaene et al., 2003).

However, it seems unlikely that the many continuous dimensions that we can compare each have a dedicated cortical territory. Therefore, another possibility is that the intraparietal region is partially involved in generic processes of comparison and internal transformation of quantitative information that can operate on many different dimensions. Comparative judgements would then lead to intraparietal activation regardless of which type of continuum is being compared. Behavioral support for the hypothesis of a generic comparison process arises from the finding of a similar distance effect with many continua, not just the number domain. The convex-upward function that relates comparison time to distance on the continuum is similar when judging non-numerical perceptual or imaginable features such as line length (Johnson, 1939), size of named objects, animals, or countries (Moyer, 1973; Paivo, 1975), and even abstract features such as ferocity or intelligence of animals (Banks and Flora, 1977).

A few neuroimaging studies have examined activation during comparisons of various continua. The results were mixed. A common right intraparietal focus was reported by Faillenot et al. (1998) for judgments of size and orientation. Fias et al. (2003) found a left intraparietal region common to the comparison of Arabic numerals, line lengths, and angles. Fullbright et al. (2003) also observed overlapping intraparietal activation for judgments of letter, number, and size ordering, though with slightly different localizations for distance effects along those three continua. Finally, Thioux et al. (2002) found intraparietal activation during number comparison, but not during comparison of the ferocity of animals.

One possible explanation for those discrepancies may reside in the choice of the compared dimensions. The parietal lobe may be particularly engaged in computations relative to space, time, and number (Walsh, 2003). The joint coding of spatial and numerical dimensions in parietal cortex might explain why physical size, spatial

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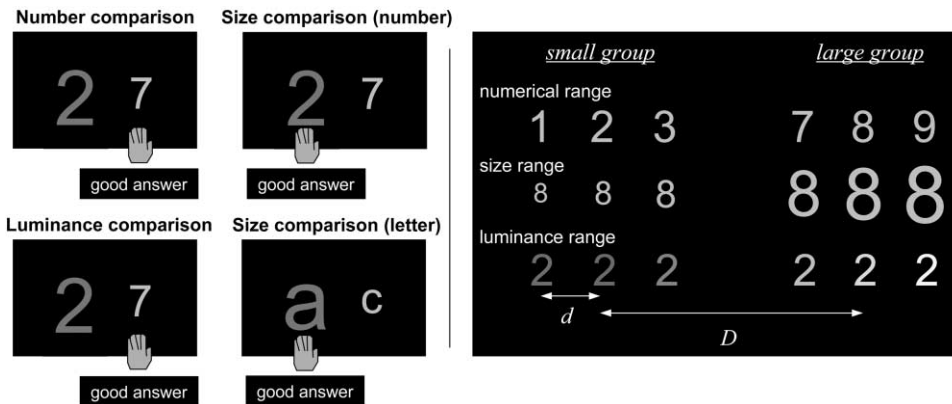


Figure 1. Stimuli and Experimental Procedure

Left: examples of stimuli and correct responses for each of the four comparison tasks. Right: range of values for each dimension. Close pairs of stimuli were composed of either two small items or two large items (hence separated by a small distance d or $2d$). Far pairs were composed of one small and one large item (separated on average by the large distance D). For each dimension, d and D were slightly modified for each subject to equate task difficulty across dimensions (see Experimental Procedures).

location, and number interfere behaviorally (Henik and Tzelgov, 1982; Dehaene et al., 1993), and why there are joint deficits of spatial and numerical bisection in parietal brain-lesioned patients (Zorzi et al., 2002). Comparison of other nonspatial visual dimensions such as color or luminance, however, may involve the ventral rather than the dorsal visual stream (McKeefry and Zeki, 1997). Such an anatomical segregation might explain why, in a behavioral task, an irrelevant number interferes with left/right orientation judgements but not with color judgements (Lammertyn et al., 2002).

To test those possibilities, we investigated the cerebral circuits for comparative judgements of Arabic numerals and two other nonnumerical dimensions, one spatial (physical size) and the other nonspatial (luminance). Fifteen subjects were scanned using a fast event-related fMRI paradigm while performing comparisons of size, luminance, and number. In all three blocks, performance was equated and identical stimuli were used, consisting of pairs of Arabic digits that varied in actual physical size, numerical size, and luminance (Figure 1). This design allowed identification of changes in activation as subjects successively focused on each dimension. It also allowed us to examine the interference evoked by the other two irrelevant dimensions, and its cerebral substrates. A fourth block, in which letters varying in size and luminance were presented, served as a control with virtually identical stimuli but no numerical magnitude.

Results

Overall Task Performance and Activation

The subject-by-subject stimulus adjustment procedure was successful in matching response times (RT) across tasks. The mean RT of correct responses (<1500 ms) was similar across tasks (560 ms for number comparison, 558 ms for size comparison of numerical stimuli, 568 ms for luminance comparison, and 542 ms for size comparison of letter stimuli). There was no task effect on RT [ANOVA $p = 0.287$, $F(3,42) = 1.30$]. A small but

significant effect was observed on error rates [respectively, 2.7%, 6.5%, 9.0%, and 4.6%; $p < 0.001$, $F(3,42) = 14.29$].

In fMRI, relative to rest, the four tasks led to a set of activations in bilateral occipitotemporal, parietal, and precentral areas ($p < 0.01$) (Figure 2). Significant overlap between these tasks (each at $p < 0.01$) was observed in the bilateral anterior IPS, close to its junction with the postcentral sulcus, and in bilateral occipital and inferotemporal areas (approximates coordinates: $-52, -32, 46$ and $47, -25, 42$ for left and right IPS, respectively; $-42, -69, -16$; $32, -60, -19$; $-23, -57, -20$ for the main occipital foci). Only four between-tasks contrasts gave significant results ($p < 0.01$). Number comparison, relative to size comparison, yielded larger activation in two bilateral inferior parietal foci ($-64, -28, 40$; $52, -28, 48$), the left IPS (extending between $-28, -48, 48$ and $-36, -48, 40$), and a left ventral temporal focus ($-52, -52, -12$). Size comparison with numerical stimuli lead to small clusters of activation in the caudate nucleus ($-12, 16, 4$) when compared to the numerical task, in the right IPS ($32, -44, 36$) and left inferotemporal cortex ($-44, -68, -4$) when compared to the luminance task, and in the right motor cortex ($32, -20, 68$) when compared to the size task with letter stimuli.

Analysis of Distance Effects

For each task, only the relevant dimension induced a distance effect on response times (Figure 3A). During number comparison, RT varied with numerical distance only [$RT_{\text{close}} - RT_{\text{far}} = 54$ ms; $p < 10^{-4}$, $F(1,14) = 97.4$]. During size comparison with numerical stimuli, only a size distance effect was observed [$RT_{\text{close}} - RT_{\text{far}} = 88$ ms; $p < 10^{-4}$, $F(1,14) = 112.7$]. The size comparison with letter stimuli also presented a similar size distance effect [$RT_{\text{close}} - RT_{\text{far}} = 87$ ms; $p < 10^{-4}$, $F(1,14) = 112.7$]. Finally, during luminance comparison, RT varied with luminance distance only [$RT_{\text{close}} - RT_{\text{far}} = 85$ ms; $p < 10^{-4}$, $F(1,14) = 87.8$].

Similarly in fMRI, distance along a given dimension affected brain activation only when subjects were attending to that dimension (Figure 3 and Table 1 for Talai-

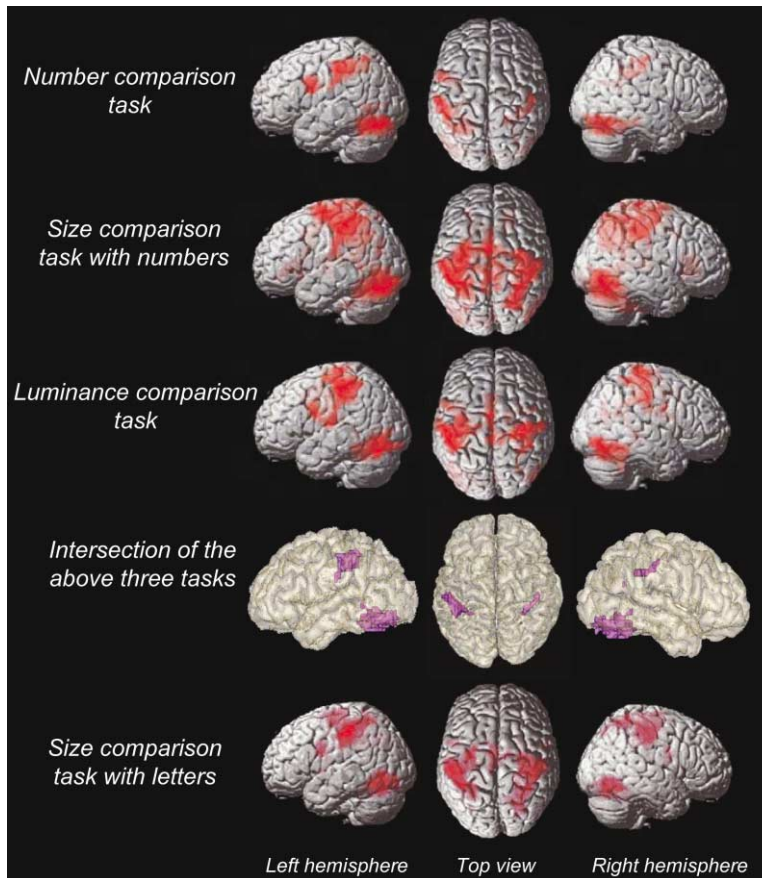


Figure 2. Overall Task Activations Relative to Rest

The first three maps reflect the three comparison tasks made on identical sets of numerical stimuli (random-effect analysis, voxel level $p < 0.01$, cluster level $p < 0.05$ corrected). Overlap of the three tasks is displayed in the fourth map, which corresponds to the Boolean intersection of the corresponding maps. The last map shows the activity during size comparison with letter stimuli (random-effect analysis, voxel level $p < 0.01$, cluster level $p < 0.05$ corrected).

each coordinate). During the number comparison task, the numerical distance effect was associated with the bilateral horizontal segment of the intraparietal sulci (HIPS) and the left precentral gyrus (see Figure 4A for details). During the luminance comparison task, a luminance distance effect was found in anterior cingulate cortex (ACC), bilateral precentral gyri, bilateral posterior intraparietal sulci, bilateral fusiform gyri, and right inferotemporal gyrus. During size comparison with number stimuli, correlates of the size distance effect were found predominantly in the right hemisphere, in the right inferior frontal gyrus, right precentral gyrus, and a large extent of the right intraparietal sulcus, but also in the left posterior intraparietal sulcus and in a posterior occipital region at the border between cerebellum and lateral fusiform and lingual gyri. Size comparison with letter stimuli gave similar results (Figure 3B), with a few additional activations in the bilateral inferotemporal gyri, the left HIPS, the left precentral gyrus, and the parahippocampal gyrus. Given this convergence, we defined the neuroimaging correlates of the size distance effect by pooling across the blocks with different stimuli (numbers or letters), and masking by each of the two size distance effects (voxelwise threshold of $p = 0.05$, clusterwise $p = 0.05$ corrected for multiple comparisons). The resulting activations were found in the bilateral precentral, intraparietal, and occipitotemporal regions and the left cerebellum, with dominant activation in the right IPS (Figure 3B).

Figure 4B shows the relative locations and Boolean

intersections of the correlates of the three distance effects (see Experimental Procedures). Bilateral regions in the depth of the anterior IPS were shared between numerical and size distance effects (approximate coordinates: 34, -43, 41 in right IPS and -42, -45, 42 in left IPS). Size and luminance distance effect overlapped in two bilateral posterior intraparietal sites (right = 28, -71, 31; left = -28, -72, 31), two bilateral inferotemporal areas (right = 42, -63, -10; left = -44, -65, -10), and the right precentral gyrus (43, -1, 27). Finally, the left precentral gyrus (-51, 4, 30) was common to numerical, size, and luminance distance effects. Those results should be interpreted with caution, however, because pairwise comparisons did not reveal any regions with a significantly greater distance effect for one dimension than for the other at conventional significance levels.

To describe in greater details the sensitivity of the parietal lobe to the three different distance effects, we plotted the three distance effects in the anterior and posterior intraparietal regions of overlap (Figure 4C). An ANOVA confirmed the significance of the size distance effect in the four parietal sites ($p = 0.048$ for the left HIPS, $p = 0.001$ for the right HIPS, $p = 0.03$ for the left posterior IPS, and $p < 0.001$ for the right posterior IPS) with a significant right hemisphere lateralization (size distance effect \times hemisphere in the posterior parietal sites; $p < 0.001$). Similar results, though without lateralization, were found for the numerical distance effect ($p = 0.001$ for the left HIPS, $p = 0.003$ for right HIPS, $p = 0.039$ for the left posterior IPS, and $p = 0.025$ for the right

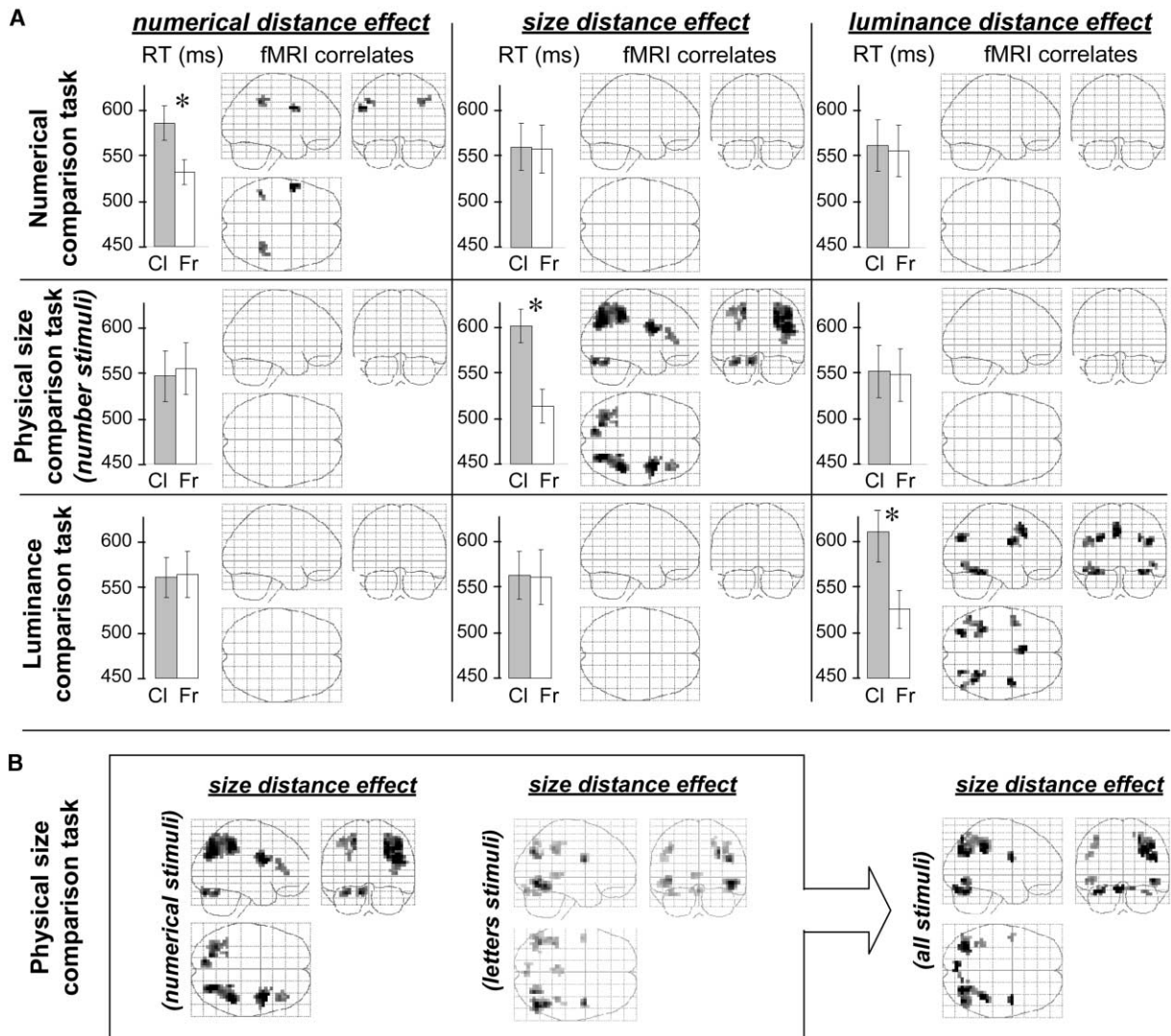


Figure 3. Behavioral and fMRI Analysis of the Distance Effects

(A) Response time to close (gray column) and far (white column) distances along task-relevant and task-irrelevant dimensions. An asterisk indicates a significant distance effect at $p < 0.001$. Glass-brain views show the neural correlates of the corresponding distance effect (close trials contrasted to far trials: voxel level $p < 0.01$, cluster level $p < 0.05$ corrected, masked by the respective overall task activation map thresholded at $p < 0.05$).

(B) Correlates of the physical size distance effect during size comparison of letter and number stimuli (see text for details).

posterior IPS). Finally, the luminance distance effect did not reach significance in the HIPS ($p = 0.086$ for the left HIPS and $p = 0.224$ for right HIPS) but was highly significant for the bilateral posterior IPS ($p < 0.001$). No significant difference between distance effects was detected in anterior HIPS. Only in the left posterior IPS did the luminance distance effect tend to be larger than the numerical distance effect ($p = 0.056$).

Interference among Dimensions

We tested the behavioral interference between two dimensions by examining whether RTs were slower on incongruent target pairs (e.g., when the numerical larger digit was physically smaller or less bright) than on congruent pairs (Figure 5). During number comparison, there was significant interference with physical size [Incongruent – Congruent = 66 ms, $p < 10^{-4}$, $F(1,14) =$

121.83] and a significant but much smaller interference with luminance [16 ms, $p = 0.005$, $F(1,14) = 11.26$]. During size comparison with numerical stimuli, there was significant interference with numerical size [48 ms, $p = 0.001$, $F(1,14) = 32.44$] and with luminance [60 ms, $p < 10^{-4}$, $F(1,14) = 68.75$]. The size-luminance interference was replicated during size comparison of letter [60 ms, $p < 10^{-4}$, $F(1,14) = 45.12$]. Finally, during luminance comparison, there was significant interference with physical size [69 ms, $p < 10^{-4}$, $F(1,14) = 65.15$], but no interference with number [5 ms, $F(1,14) = 0.26$]. Thus, the main findings indicated symmetrical interference effects between number and size and between size and luminance.

In fMRI, the contrast between incongruent and congruent trials in each task revealed the cerebral correlates of behavioral interference effects (see Figure 5 and Table

Table 1. Cerebral Correlates of Distance Effects with Various Continuous Dimensions

Task	Coordinates			Z Score	Brain Area
	x	y	z		
Numerical comparison	-48	4	32	3.64	left precentral gyrus
	-44	-44	40	2.90	left intraparietal sulcus
	36	-44	40	2.75	right intraparietal sulcus
Size comparison (numbers)	44	8	24	4.37	right precentral gyrus
	28	-72	40	4.20	right posterior intraparietal sulcus
	40	-40	44	3.85	right intraparietal sulcus
	-12	-80	-24	3.53	left lingual gyrus/cerebellum
	-20	-72	52	3.45	left posterior intraparietal sulcus
	-32	-64	-24	3.38	left lateral fusiform gyrus/cerebellum
	44	28	16	3.00	right inferior frontal gyrus
Luminance comparison	-4	16	40	4.04	anterior cingulate gyrus
	-28	-72	32	3.88	left posterior intraparietal sulcus
	40	-56	-16	3.70	right fusiform gyrus
	40	-4	28	3.63	right precentral gyrus
	-32	-44	-16	3.45	left fusiform gyrus
	28	-72	28	3.35	right posterior intraparietal sulcus
	48	-72	-8	3.18	right inferior temporal gyrus
	-40	4	28	3.01	left precentral gyrus
	48	-68	-8	4.35	right inferior temporal gyrus
	28	-72	36	3.82	right posterior intraparietal sulcus
Size comparison (letters)	44	0	24	3.78	right precentral gyrus
	-40	-64	-4	3.54	left inferior temporal gyrus
	0	-84	-20	3.23	gyrus lingual/cerebellum
	-40	-44	40	3.15	left intraparietal sulcus
	36	-40	36	3.09	right intraparietal sulcus
	-40	-72	-20	2.96	left lateral fusiform gyrus/cerebellum
	-8	-40	4	2.85	parahippocampal gyrus
	-48	-4	32	2.76	left precentral gyrus
	32	-72	36	3.83	right posterior intraparietal sulcus
	40	-40	44	3.59	right intraparietal sulcus
Size comparison (all stimuli)	-8	-80	-20	3.71	left lingual gyrus/cerebellum
	40	0	28	3.57	right precentral gyrus
	-36	-68	-24	3.57	left lateral fusiform gyrus/cerebellum
	44	-72	-8	3.36	right inferior temporal gyrus
	32	-64	-24	2.90	right lateral fusiform gyrus/cerebellum
	-36	-52	52	2.82	left intraparietal sulcus
	-52	-72	-8	2.81	left inferior temporal gyrus
	16	-64	60	2.69	right precuneus
	-48	0	28	2.64	left precentral gyrus

2 for Talairach coordinates). During number comparison, interference from physical size enhanced activity in left parietal and left premotor cortices and right cerebellum. Symmetrically, during size comparison, interference from numerical size activated the same regions, plus additional activation in right visual extrastriate and anterior cingulate cortices. When we pooled the two blocks together, number/size interference resulted in bilateral parietal, left premotor, and cerebellar activations. During the luminance task, interference from the irrelevant dimension of size activated a different set of areas: left lateral occipito-temporal areas and the right inferior frontal gyrus. Conversely, during the size comparison task, either with number or with letter stimuli, no areas showed a significant interference from luminance. No area reached significance when size/luminance interference was investigated by pooling together the luminance and size tasks.

Discussion

We investigated the cerebral substrates of comparative judgements on three different dimensions: number size, physical size, and luminance. The stimuli were identical

in all conditions, and the behavioral performance was matched by adjusting the stimuli on an individual basis during the training period. As a result, in the three comparison tasks, response times showed similar gradients of difficulty determined by the distance of the compared items on the relevant continuum. However, an indication that the three dimensions are not processed identically came from the analysis of interference effects. Significant interference was observed between number and size, as well as between size and luminance, but little or no interference was found between number and luminance. This suggests the presence of some convergence between processing streams for number and size on the one hand, and for size and luminance on the other. We attempted to identify the cerebral substrates of such convergence using fMRI.

A first examination of each comparison task relative to rest showed a similar pattern of bilateral parietal, precentral, and occipitotemporal activation for all tasks, regardless of the judged dimension (number, size, or luminance) and of the stimuli (numbers or letters). Intersection analysis revealed that the bilateral intraparietal sulci and occipitotemporal regions were common to all tasks. This global activation pattern fits with earlier re-

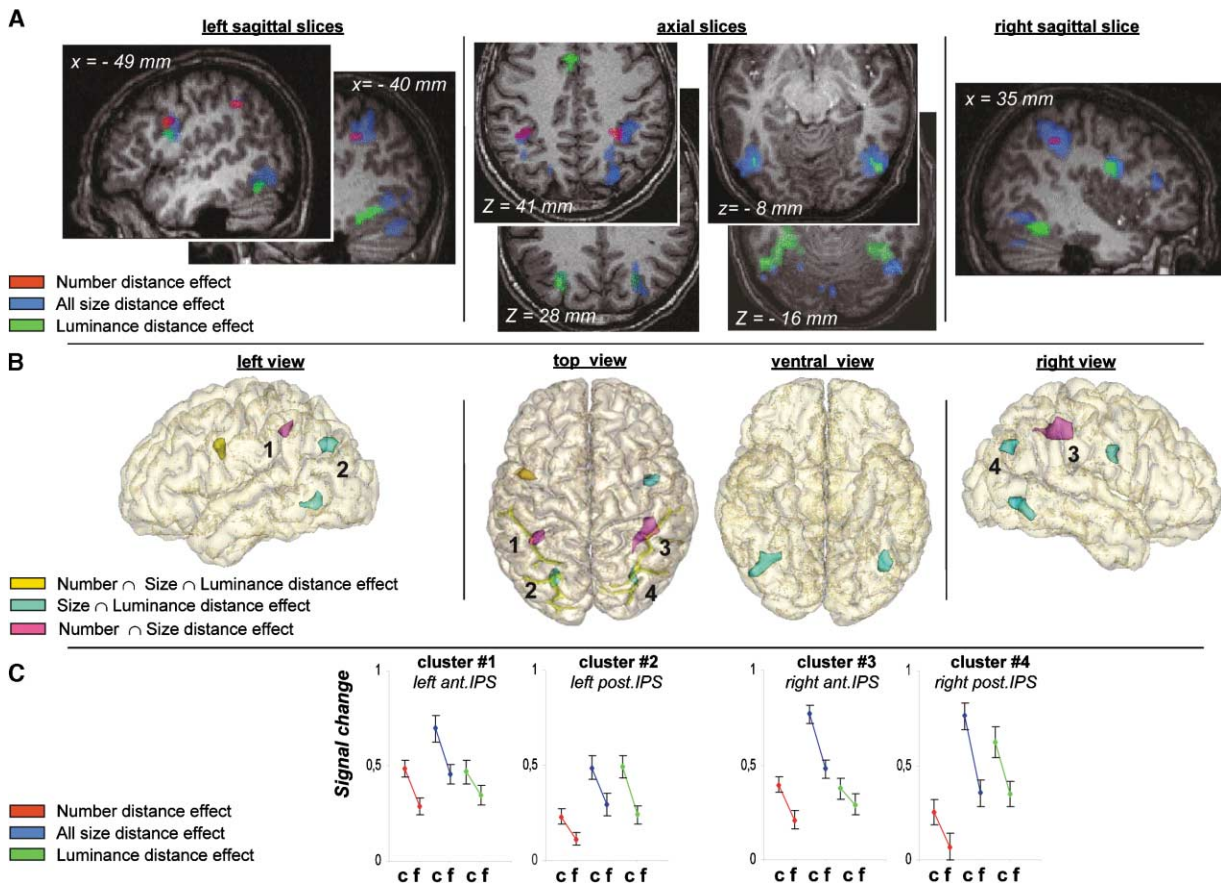


Figure 4. Neural Correlates of the Three Distance Effects and Their Anatomical Overlap

(A) Sagittal and axial views of voxels showing a distance effect for number (red), size (blue), and luminance (green) superimposed on the anatomy of one subject.

(B) Boolean intersections of images of the distance effects superimposed on a translucent three-dimensional model of the cortical surface of one subject (intersections were thresholded at $p < 0.05$ for a better visualization). Light yellow indicates bilateral intraparietal sulci on the top view

(C) BOLD signal relative to rest for the close (c) and far (f) conditions, plotted for the three relevant distance effects (number distance effect in number task in red, size distance effect in size task in blue, and luminance distance effect in luminance task in green) within the anterior and posterior parietal clusters of overlap (numbering of clusters as in B).

sults, which emphasized the role of the intraparietal sulcus in comparison tasks (Chochon et al., 1999; Faillenot et al., 1998; Fias et al., 2003; Fullbright et al., 2003). During number comparison relative to letter naming, in particular, Chochon et al. (1999) observed a right parietal site next to the postcentral gyrus (42, -24, 45), very close to the right parietal site found common to all comparison tasks in the present work (47, -25, 42).

Finer-grained analysis of the neural correlates of the distance effect revealed a trend toward regional organization. When subjects compared stimuli for number, size, or luminance, distance on that dimension modulated activation in partially overlapping brain regions. Numerical distance modulated activation in the bilateral anterior IPS and left precentral cortex. Size distance modulated activation in a more posterior region of the IPS as well as in bilateral precentral, inferior temporal, and cerebellar regions. Finally, luminance distance modulated activation in a very posterior sector of the IPS as well as bilateral precentral, inferior temporal, and anterior cingulate regions.

In our study, no region appears specific for a given dimension, in the sense of exhibiting a significantly greater distance effect for one dimension than for the others. Nevertheless, the location of activation peaks for each dimension is congruent with previous work. The finding of a numerical distance effect in the right anterior horizontal segment of the intraparietal sulcus (HIPS) replicates earlier results on numerical comparison, with very similar peak coordinates (Talairach coordinates: 36, -44, 40 in the present study; 48, -36, 39 in Pinel et al., 1999; 40, -44, 48 in Pinel et al., 2001). The present coordinates also coincide precisely with those reported in a recent meta-analysis of activations during number processing (Dehaene et al., 2003). The HIPS is systematically activated in conditions that emphasize quantity processing, for instance approximate versus exact addition (Stanescu-Cosson et al., 2000), computation of subtractions versus rote retrieval of multiplication facts (Lee, 2000), or even the mere detection of a single digit versus the detection of a letter (Eger et al., 2003).

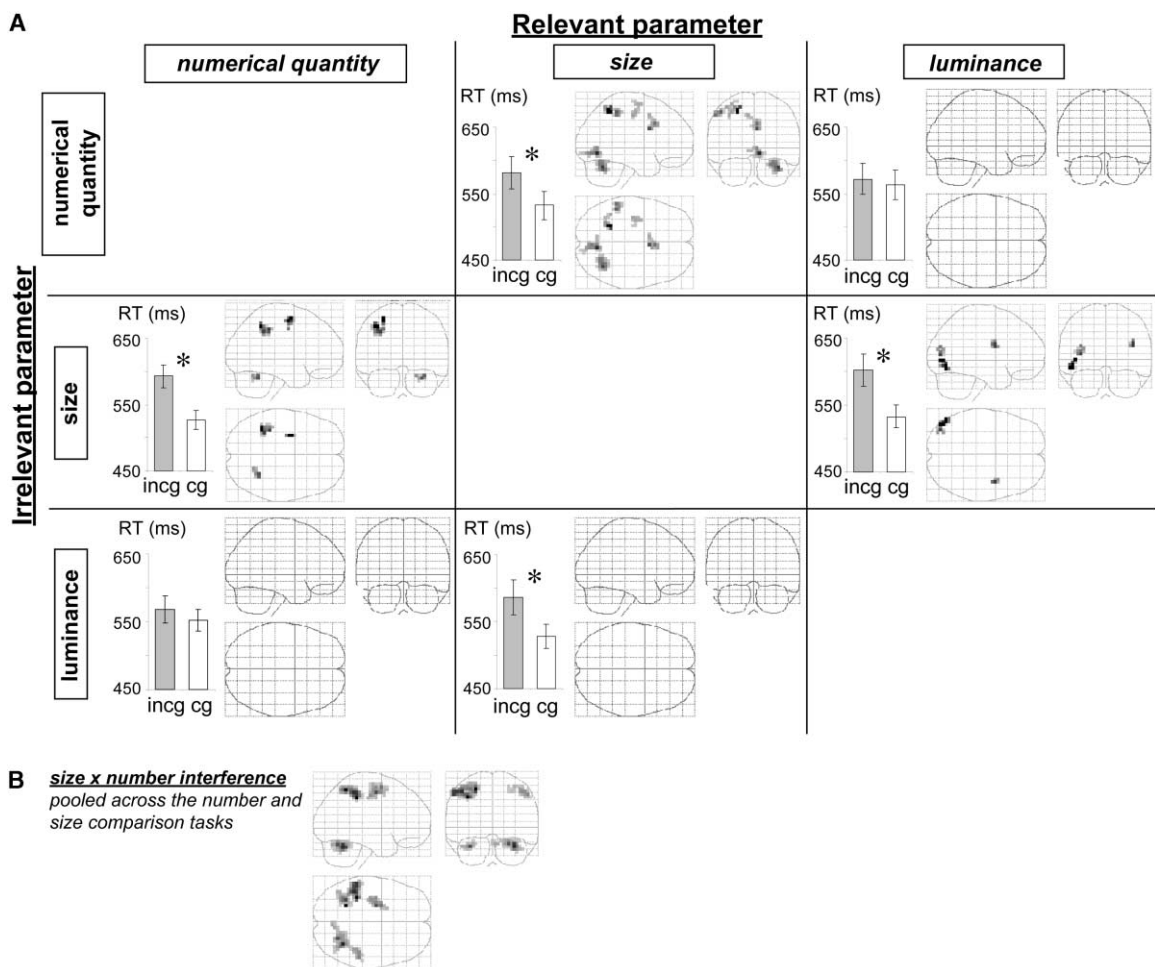


Figure 5. Behavioral and fMRI Analysis of the Interference between Dimensions

(A) Columns represent the mean RTs (in ms) as a function of whether the relevant and irrelevant dimensions were incongruent (gray column) or congruent (white column). An asterisk indicates a significant interference effect at $p < 0.001$. Glass-brain views show the neural correlates of the corresponding interference (greater activation for incongruent than for congruent trials: voxel level $p < 0.01$, cluster level $p < 0.05$ corrected, masked by the respective overall task activation map thresholded at $p < 0.05$).

(B) Correlates of interference between numerical and physical size pooled across the number and size comparison tasks.

A novel result of the present study is that the HIPS, particular in the right hemisphere, is also activated during comparisons of physical size, with a size distance effect comparable to the numerical distance effect. Thus, this region is not devoted exclusively to number processing but is engaged whenever subjects attend to the dimension of size, whether numerical or physical. The finding of an overlapping representation for physical and numerical size fits with the recent observation of joint deficits of spatial and numerical bisection in right-parietal neglect patients (Zorzi et al., 2002). Indeed, fMRI of the line bisection tasks yielded a strong activation of the right IPS and cerebellum, at coordinates similar to ours (Fink et al., 2002). Altogether, these findings fit with the hypothesis that numerical and spatial magnitudes are jointly represented in parietal cortex (Walsh, 2003), perhaps in the form of a mental “number line” (Dehaene et al., 1993).

The engagement of posterior parietal cortex in size judgements fits with previous reports of its involvement

in various visuospatial tasks, for instance matching angles made by hands of two imagined clocks (Trojano et al., 2000), discrimination of spatial properties such as size and orientation (Faillenot et al., 1998), or mental rotation of different visual objects (Jordan et al., 2001). In particular, a parametric study of mental rotation task (Harris et al., 2000) similar to ours studied the cerebral correlates of the angular distance effect in a mental rotation task with 3D objects. The regular increase of RTs with angular distance was correlated with activation in a small area located in the right posterior lobe (30, -68, 44), very close to the site reported here for the distance effect during size judgment.

Finally, an overlap between the distance effects for luminance and physical size was observed in a set of bilateral occipito-temporal and posterior intraparietal regions. An important commonality between luminance and size comparisons is that in both cases, the source of difficulty arises from the necessity of attending to increasingly finer perceptual details of the stimuli (either

Table 2. Cerebral Correlates of Cross-Dimensional Interference

Task	Coordinates			Z Score	Brain Area
	x	y	z		
Number/size interference (numerical task)	-36	-48	48	3.28	left intraparietal sulcus
	-28	-4	60	3.27	left premotor cortex
	28	-52	-28	2.92	right cerebellum
Number/size interference (size task)	-24	-52	52	3.74	left superior parietal lobule
	8	-68	-8	3.41	extrastriate occipital cortex
	36	-60	-28	3.32	right cerebellum
	4	8	28	3.23	anterior cingulate cortex
	-48	-40	52	3.17	left intraparietal sulcus
	-36	-16	48	2.72	left post-central cortex
Number/size interference (numerical and size tasks)	-36	-36	44	4.06	left intraparietal sulcus
	32	-56	-28	3.69	left cerebellum
	-24	-8	52	3.52	left premotor cortex
	-32	-52	-28	3.52	right cerebellum
	52	-32	48	3.12	right inferior parietal lobule
	-44	-76	0	3.23	left lateral occipitotemporal gyrus
Size/luminance interference (luminance task)	40	0	20	2.97	right inferior frontal gyrus
	-36	-80	8	2.93	left medial occipital gyrus

shades of gray or small differences in size). This aspect sets those two tasks apart from the numerical task with Arabic digits, in which the source of the difficulty arises from the semantic rather than the perceptual level. Given that the stimuli were identical, the observed occipito-temporal activations reflect an attentional amplification of the relevant perceptual parameter within extrastriate visual cortex, as previously reported for attention to color, movement, or shape (Corbetta et al., 1991). The posterior parietal activations may represent the source of this attention effect, since they have been reported at an identical location during a variety of top-down attention tasks (Wojciulik and Kanwisher, 1999; Simon et al., 2002).

In our data, the only region that showed significant effects of distance along all three dimensions of number, size, and luminance was the left precentral gyrus. Similar precentral activations have been described in other numerical tasks (Chochon et al., 1999; Pesenti et al., 2000). Pesenti et al. (2000) proposed that they reflect the fact that number knowledge developed from finger knowledge. This idea might be extended to size processing, considering that object size information is needed to adjust finger position during grasping. However, it cannot explain the involvement of the precentral gyrus in the luminance distance effect. Rather, we propose that this region is involved in response selection and decision requirements common to all three comparison tasks. Precentral cortex would receive information from the relevant posterior systems and accumulate evidence in favor of the larger or smaller decision, as postulated in mathematical models of comparison (Link, 1990).

A striking aspect of the pattern of overlap between distance effects is that it matches the pattern of interference in response times. At the cortical level, number and size dimensions overlapped in the anterior HIPS, while size and luminance overlapped in the posterior IPS and ventral occipito-temporal cortex; however, there was no posterior region of overlap between number and luminance. Similarly at the behavioral level, interference was observed between number and size, as well as between size and luminance, but subjects could

selectively attend to luminance without suffering from incongruent variations in number, and vice versa. Thus, the anatomical proximity between the neural structures activated by the relevant and irrelevant dimensions correlated with the amount of cross-dimensional interference in behavior (Lammertyn et al., 2002; Fias et al., 2001). We tested this idea directly by examining, for each pair of relevant and irrelevant dimensions, which brain areas showed a greater activation on incongruent than on congruent trials. The results were highly consistent with the overlap analysis: parietal, premotor, and cerebellar areas showed number-size interference, while left occipitotemporal and right precentral cortex showed size-luminance interference. This analysis thus demonstrates that behaviorally similar interference effects may have quite different neural origins. Our results suggest that size and luminance were both coded within the ventral visual stream, thus creating a partial confusion between those two perceptual dimensions that propagated to the precentral decision-related area. Indeed, the left precentral gyrus is thought to play a role in the management of interference (Zysset et al., 2001; see also Gruber et al., 2001), and a single-neuron study in primates has demonstrated the presence of neural activity induced by an irrelevant perceptual dimension (color or motion) within prefrontal cortex during a binary decision task (Lauwereyns et al., 2001). Our results also suggest, however, that number-size interference originates from a different mechanism. Although initially conveyed by distinct symbolic and nonsymbolic codes, number and size appear to converge at an abstract representational level toward a partially overlapping representation in parietal cortex. Indeed, the finding of significant number/size interference in both behavior and fMRI provides positive evidence that the internal representations of number and size are not merely juxtaposed anatomically but share common neural resources.

In summary, our study demonstrates that, during comparative judgements, continuous dimensions such as luminance, size, and number are neither processed by a parcellation of highly specialized cortical subregions, nor by a single generic comparison system. The model

most compatible with our results is that of a distributed coding along the length of the intraparietal sulcus, with partially different local peaks for each dimension (Figure 4A), but also considerable interdimensional overlap and with convergence toward precentral cortex (Figure 4B). Individual parietal neurons may encode stimuli along a single dimension, as exemplified by the discovery of neurons tuned to number in both prefrontal and parietal cortex (Nieder et al., 2002; Sawamura and Shima, 2002). Nevertheless, the present results suggest that such neurons are unlikely to be grouped within a unique, well-delimited anatomical area. More plausibly, they may be intermingled and distributed along the IPS, with local changes in density creating a progressive shift in peak activation when measured with the coarse resolution of fMRI. The proposed distributed overlapping code for continuous dimensions in IPS is analogous to the distributed and overlapping coding of object categories in the ventral occipito-temporal region (Haxby et al., 2001), where no single region is uniquely selective for faces or houses, but where local biases in object representation are evident and identical across subjects (Hasson et al., 2003).

Experimental Procedures

Participants

Fifteen healthy French volunteers (9 females, 6 males, mean age 23.7) participated in the study, after giving their written consent to the protocol, which was approved by the regional ethical committee (Hôpital de Bicêtre, France). All were right handed as confirmed by means of the Edinburgh inventory and had normal or corrected-to-normal vision.

Imaging Procedure

Cerebral images were acquired on a 3T MRI system (Bruker, Germany) with a fast event-related design (repetition time = 2.4 s). Functional images sensitive to blood oxygen level-dependent (BOLD) contrast were obtained with a T2*-weighted gradient echo-planar imaging sequence [TE (echo time) = 40 ms, angle = 90°, FOV (field of view) = 192 × 256 mm, matrix = 64 × 64]. Whole-brain volumes were acquired in 26 slices with a thickness of 4.5 mm. Acquisition of the first slice of each volume was synchronized with stimulus onset. High-resolution anatomical images [3D gradient echo inversion-recovery sequence, TI (inversion time) = 700 ms, FOV = 192 × 256 × 256, matrix = 256 × 128 × 256, slice thickness = 1 mm] were also acquired.

Tasks and Stimuli

Each subject performed, in a random order, four comparison tasks in four different blocks. For three of these blocks, stimuli were pairs of numbers (small numbers: 1, 2, 3; and large numbers: 7, 8, 9) presented visually on a rear-projection screen (70 Hz refresh rate) at a rate of one pair every 2.4 s. Before each block of 160 trials, subjects were instructed to compare stimuli either according to their numerical value, their physical size, or their luminance. On each trial, two stimuli appeared simultaneously on the left and right side of the screen (2° left and right of fixation) during 200 ms followed by a black screen for 2200 ms. Subjects responded by pressing the left or right button to indicate the side of the largest relevant attribute (see examples in Figure 1). For the fourth block, stimuli were letters (six vowels: a, e, i, o, u; and five consonants: c, n, r, s, v) with irrelevant variations in luminance, and subjects had to perform only a physical size comparison. Each block was preceded by six training trials.

To study the numerical distance effect, we selected target pairs made of close digits (1-2, 2-3, 1-3, 7-8, 7-9, 8-9) and target pairs made of far digits (1-7, 1-8, 2-7, 2-9, 3-8, 3-9). These pairs were formed by combinations of two triplets (1-2-3 and 7-8-9), so that

each digit from each triplet appeared with equal frequency in the close and far pairs. The structure of these pairs can be entirely described by the minimum value m (here number 1), the distance between digits within a triplet (d , here equal to 1), and the between-triplet distance (D , measured as the distance between corresponding elements of the triplets, and here equal to 6). We then applied this generic structure to target pairs for the physical size and luminance comparison tasks by selecting, for both dimensions, a minimum value m , a within-triplet distance d , and a between-triplet distance D . To equate difficulty across the four tasks, during a training session of about 1 hr performed both outside and inside the fMRI scanner, the experimenter progressively adjusted the parameters separately for physical size (defined by the point size of the character font) and luminance (from 0 to 255 in RGB-coded shades of gray) to obtain similar mean reaction times and distance effects for each task. Those parameters were then fixed for the imaging session. The following mean parameters were used; for size, $m = 38.3 \pm 0.33$, $d = 8.3 \pm 0.33$ (= 2.9° of visual angle), $D = 30.2 \pm 0.74$ (= 10.5° of visual angle), and for luminance, $m = 145.4 \pm 1.48$, $d = 23.07 \pm 0.55$, $D = 83.87 \pm 1.35$ (see examples in Figure 1).

During each task, stimuli were constructed as a random combination of pairs of parameters from the lists of numerical, size, and luminance values selected as described above. We prescribed an identical number of left versus right hand response trials, and congruent versus incongruent trials for all relevant and irrelevant pairs of dimensions, thus defining a 2 (hand) × 2 (size/number congruence) × 2 (size/luminance congruence) × 2 distance (close/far distance) orthogonal design, each repeated eight times. We added 20% of randomly distributed rest trials, during which subjects fixated a visual cross in the middle of the screen without responding, thus resulting in 160 trials per block. The experiment was programmed using the E-Prime software (Psychology Software Tool, Inc.).

Image Processing and Data Analysis

Functional images were analyzed with statistical parameter mapping software (SPM99, <http://www.fil.ion.ucl.ac.uk/spm>). Each block contained 160 brain volumes after rejecting the first six scans. Functional images were realigned to the first scan of the experimental session (closest to the anatomical image), corrected for spatial distortion and slice acquisition delays, and normalized to the MNI template using an affine transformation and voxels of 4 × 4 × 4 mm³. Images were spatially smoothed using a Gaussian kernel of 5 mm FWHM. A model of the fast event-related BOLD time course was designed using the standard hemodynamic response function (HRF) of SPM and its derivative. A temporal bandpass filtering was applied (high-pass cut off of 32 s, low-pass 4 s Gaussian filter).

In a first analysis, we sorted for each task the target pairs into 8 conditions (close versus far numbers × close versus far sizes × close versus far luminances) to test for all possible relevant and irrelevant distance effects. All activations were isolated using a random effect analysis of individual contrasts (smoothed with a kernel of 5 mm). We first isolated the circuits involved in each comparison task by contrasting correct trials to the rest trials of the same block at a voxelwise threshold fixed at $p < 0.01$ and a clusterwise threshold fixed at $p < 0.05$ corrected for multiple comparisons across the brain volume. This image, thresholded at $p < 0.05$, also served as a mask for the detection of between-tasks differences, distance effects, and interference effects. We compared the activations between tasks using appropriate interaction terms (e.g., (task1 – rest1) – (task2 – rest2)), and the functional imaging correlates of the distance effect using a contrast of close trials versus far trials. We examined differences between distance effect by testing the significance of the interactions (close – far trials for dimension i) – (close – far trials for dimension j). To determine the areas of overlap between distance effects, we performed Boolean intersections of their corresponding images, each at a voxelwise threshold of $p < 0.01$ and a corrected clusterwise threshold of $p < 0.05$. Three-dimensional representations of overlap in the brain were obtained using Anatomist (<http://brainvisa.free.fr/index.html>), a visualization software developed in our lab.

In a second analysis, we sorted trial pairs into 4 conditions (congruent versus incongruent trials for size and number, and congruent

versus incongruent trials for size and luminance) to test for all possible relevant and irrelevant effects of interference. Random effect analyses isolated the regions involved in cross-dimensional interference in each task by contrasting incongruent trials to the congruent trials, at a voxelwise threshold of $p < 0.01$ and a clusterwise threshold of $p < 0.05$ corrected for multiple comparisons across the brain volume.

We selected a relatively permissive voxelwise threshold of $p < 0.01$ because we were looking for the cerebral correlates of small behavioral distance effects (range 54–112 ms), which were expected to result in small changes in the fMRI activation. Combined with $p < 0.05$ corrected at the cluster level, this analysis should not lead to a greater number of false positives than the usual analysis at $p < 0.001$, but permits the detection of relatively large areas of activation with a relatively small difference between conditions.

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